Development of space perception in relation to the maturation of the motor system in infant rhesus macaques (*Macaca mulatta*)

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Abstract

To act on the environment, organisms must perceive object locations in relation to their body. Several neuroscientific studies provide evidence of neural circuits that selectively represent space within reach (i.e., peripersonal) and space outside of reach (i.e., extrapersonal). However, the developmental emergence of these space representations remains largely unexplored. We investigated the development of space coding in infant macaques and found that they exhibit different motor strategies and hand configurations depending on the objects' size and location. Reaching-grasping improved from 2 to 4 weeks of age, suggesting a broadly defined perceptual body schema at birth, modified by the acquisition and refinement of motor skills through early sensorimotor experience, enabling the development of a mature capacity for coding space.

Keywords

premotor cortex; space representation; peripersonal space; body schema; motor development

1. Introduction

A central issue in cognitive development is how the brain constructs a map of the surrounding world and how this map interacts with the internal representation of one's body. To interact with an object, it is necessary to determine whether an object is in the near-reachable space or in the far-unreachable space. The capacity to discriminate an object as reachable involves not only information about properties of objects and affordances for

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action and interaction, but also spatial information of objects and their relation to the body and the possibilities of acting (Witt, Profitt, & Epstein, 2004).

Objects in peripersonal space, that is, the space immediately surrounding the body, can be easily grasped and manipulated, whereas objects located beyond this space (i.e., extrapersonal space) cannot be reached without moving the torso towards the object. To plan appropriate behavioral patterns, the brain needs to differentiate objects situated in peripersonal space from those in extrapersonal space (Previc, 1990, 1998; Rizzolatti et al., 1988; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997). In support of this, neurophysiological experiments in adult nonhuman primates and neurologically impaired human patients reveal that the space immediately surrounding the body is represented differently than space farther away (Brain, 1941; Sommer, 1969). Furthermore, the brain has different ways of coding the position of objects placed at different locations with respect to the body (Iriki, Tanaka, & Iwamura, 1996; Làdavas, 2002; Shelton, Bowers, & Heilman, 1990).

Other neurophysiological studies in monkeys reveal additional details of how different brain areas are involved in space coding (Rizzolatti & Luppino, 2001). For example, bimodal neurons, which code for peripersonal and extrapersonal space, have been described in inferior parietal areas and the ventral premotor cortex (Duhamel, Colby, & Goldberg, 1998; Fogassi et al., 1992, 1996; Graziano & Cooke, 2006; Graziano, Yap, & Gross 1994; Graziano & Gross, 1998). These neurons are activated by visual as well as somatosensory stimulation applied to specific body parts, and exhibit higher activity when visual stimuli are within peripersonal space, compared to extrapersonal space. Recent behavioral and neuroimaging studies with healthy individuals suggest the presence of a functionally homologous space coding system in humans (Bremner, Schlack, Duhamel, Graf, & Fink, 2001; Macaluso & Maravita, 2010; Pavani & Castiello, 2004; Spence, Pavani, & Driver, 2000; Spence, Pavani, Maravita, & Holmes, 2004). Moreover, there are reports of brain-damaged patients with specific impairments in detecting information within peripersonal space, but not extrapersonal space, or *vice versa* in extrapersonal space (Brozzoli, Demattè, Pavani, Frassinetti, & Farnè, 2006; Cowey, Small, & Ellis, 1994; Farnè, Demattè, & Làdavas, 2003; Làdavas & Farnè, 2004; Vuilleumier, Valenza, Mayer, Reverdin, & Landis, 1998).

Studies in monkeys have shown that several parietal-premotor circuits work in parallel supporting sensorimotor transformation to control arm-hand movements in space. In fact, in the posterior parietal area PFG there are neurons that code not only for space, but are also active while the monkey executes a grasping action. In fact, about half of PFG neurons showing responses to visual stimuli moving in peripersonal space fired also during the active arm movement (Rozzi, Ferrari, Bonini, Rizzolatti, & Fogassi, 2008). Similar properties have been found in anatomically connected ventral premotor areas F4 and F5 (Maranesi et al., 2012). Other parietal cortical areas, located within the intraparietal sulcus (area AIP), possess neurons that are critically involved in grasping. For example, in both areas AIP and F5 there are neurons that have visuo-motor properties, firing both during the observation of objects and during grasping (Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Raos, Umiltá, Murata, Fogassi, & Gallese, 2006). Together, these and other investigations demonstrate the existence of several cortical parietal and premotor areas that code for several

aspects of actions, and suggest that neuronal visual responses related to objects and space are tightly linked with the possibility of the body to move in space and to reach targets. These circuits have been proposed to play an important role in the organization of goal-directed movements in space, and lesions to these circuits can produce several impairments in visually-guided reaching and grasping (Fogassi, Gallese, Buccino, Craighero, Fadiga, & Rizzolatti, 2001).

The link between the control of movement and space perception has been emphasized by several neurophysiological and neuropsychological studies (Matelli & Luppino, 2001; Rizzolatti, Fogassi, & Gallese, 2002). Interestingly, space coding for peripersonal and extrapersonal space appears to be dynamic in that it can be modified by active movement and sensorimotor experience. For example, tool use can change the perception of the spatial relation between the body and the object upon which the tool is acting (Berti & Frassinetti, 2000; Berti & Rizzolatti, 2002; Halligan, Fink, Marshall, & Vallar, 2003; Iriki et al., 1996; Longo & Lourenco, 2007; Maravita & Iriki, 2004; Rizzolatti, Matelli, & Pavesi, 1983; Weiss, Marshall, Zilles, & Fink, 2003). Another example is that of a patient affected by selective neglect for the space close to the body, whose symptoms were transferred into the far space after using an extension tool, as if the use of the tool remapped the far space as near-reachable space (Berti & Frassinetti, 2000).

Although developmental research on space coding is sparse, behavioral studies provide initial indications that young human infants have some spatial representation of peripersonal space when planning and executing reach movements (Clifton, Rochat, Litovsky, & Perris, 1991; Field, 1977). For example, 3-month-old human infants appear to encode locations egocentrically, showing initial evidence of a gradual shift from egocentric to object-centered references by 6 months (Gilmore & Johnson, 1997; Newcombe & Huttenlocher, 2003). It has been also reported that, between 4 and 5 months of age, human infants develop the ability to coordinate and update their spatial reference frames in relation to their capacity to lean the body forward towards objects (Yonas & Hatman, 1993). Moreover, 12-month-old human infants can use a tool to extend their spatial interaction range (McKenzie, Skouteris, Day, Hartman, & Yonas, 1993). Despite these studies highlighting important aspects of the development of space processing, the development of spatial discrimination—distinguishing peripersonal and extrapersonal space—remains largely unexplored.

Some studies have shown that infant macaques develop the capacity to reach and grasp starting from the third week of life (Lawrence & Hopkins, 1976; Nelson et al., 2011). In addition, other studies report that infant macaques' capacity to move autonomously in their surrounding environment is precocious, beginning in the first week of life (Hinde, Rowell, & Spencer-Booth, 1964; Maestripieri, 1996). This suggests that the first weeks of life are critical for the development of body maps, which support infants' capacity to move in the environment and interact with objects. Although there is a strict dependence between the development of motor skills and space representation, the relationship between these two aspects of motor development has, to our knowledge, not been thoroughly explored. In the present study, we investigated the development of space processing in rhesus macaques between the second and the fourth weeks of life. Specifically, we presented infants with objects of different sizes at different distances from the body (i.e., peripersonal and

extrapersonal space) and examined both the behavioral patterns used to reach objects and grip configurations for grasping objects.

A nonhuman primate model, and a macaque monkey model specifically, is advantageous for investigating the development of space perception. First, the neural mechanisms underpinning the control of reaching-grasping movement and space coding in humans and macaques are similar and have been described in great detail. In fact, homologue cortical areas control reaching-grasping and process peripersonal space in both species (Bremner, Schlack, Duhamel, Graf, & Fink, 2001; Macaluso & Maravita, 2010; Pavani & Castiello, 2004; Spence, Pavani, & Driver, 2000; Spence, Pavani, Maravita, & Holmes, 2004). Second, given human infants' limited response repertoire in the first few months of life, it would be difficult to investigate the development of grasping in different space sectors. In contrast, macaques have a precocious motor development, making it possible to follow each infant's motor skill development, including their grasping and locomotion in relation to their perception of space.

2. Materials and Methods

2.1. Pilot Testing

2.1.1. Subjects and Procedures—To develop a reaching-grasping task, we carried out a pilot study in the first and second weeks of infants' life, in which we tested 4 infants in their incubators, while still clinging to their surrogate, by presenting them with a large colored ball (21 mm diameter). We initially moved the ball both horizontally and vertically in front of them in order to evaluate the timing of the emergence of their ability to visually track the object and to adjust their posture. We then presented the ball in front of the infants and recorded any attempts to reach-grasp the target.

2.1.2 Preliminary Behavioral Observations—Preliminary observations revealed that from the fourth day of life all infants were able to visually track the moving object. Moreover, their capacity to cling firmly to the surrogate and move one arm in space to grasp objects improved in the first days of life, suggesting that in the first week of life important postural adjustment and coordinated visuomotor movements are emerging. However, their first attempts to reach and grasp the ball appeared only at day 7. In fact, starting from this age and across the second week of life, we scored a total of 81 reaching attempts, 51 (63%) of which ended with successful grips.

Based on these preliminary observations, we designed a task aimed at investigating the development of infants' capacity to perceive objects' size and space location.

2.2. Reaching-Grasping Task

2.2.1 Subjects and Housing—Subjects were 16 infant macaques (*Macaca mulatta*), 10 males and 6 females, followed longitudinally from age 7 to 30 days (mean infant age: week 2 $M = 10.19$ days, $SD = 1.03$, week 3 $M = 17.33$ days, $SD = .90$, week 4 $M = 24.31$ days, $SD = 1.11$). Infants were separated from their mother on day 1 post-partum and reared in a nursery facility according to procedures described by Shannon, Champoux, and Suomi (1998). Infants were individually housed in plastic incubators ($51 \times 38 \times 43$ cm) during the

first two weeks of life, and housed in metal cages ($65 \times 73 \times 83$ cm) from the third week onward. Both housing arrangements contained an inanimate surrogate mother as well as loose pieces of fleece fabric, one plush toy, and various plastic toys. During the first week of life, the surrogate mother was composed of 16.5 cm circumference polypropylene cylinder, wrapped in fleece fabric and attached by a flexible metal component to an 11.5 cm wide circular metal base. In the second week, infants were provided with a hanging surrogate mother (see also Dettmer, Novak, Meyer, Ruggiero, & Suomi, 2008), consisting of a plastic cylinder core (20 cm high and 19 cm circumference) with a wide soft cloth cover (20×25 cm). For the first month of life, infants could see and hear, but not physically touch, other infants. For further details about rearing procedures, see also Ferrari, Visalberghi, Paukner, Fogassi, Ruggiero, and Suomi (2006).

Testing was conducted in accordance with regulations governing the care and use of laboratory animals. The Animal Care and Use Committee of the National Institutes of Health approved this study.

2.2.2. Experimental Setting—For the experimental setting, we positioned a rectangular board (31.6 cm × 36.5 cm) on a table. On the board there were 7 semicircles drawn as markers to allow us to calculate the exact distance between the stimulus and the infant. Opaque vertical panels were positioned along two sides of the table to prevent the infant from seeing the person presenting the stimuli and other distractions. The panel immediately in front of the infant contained a small window, through which one experimenter presented ball stimuli to the infant (Figure 1). We recorded all sessions with two Sony Digital Video camcorders (ZR600 and HDR-CX560V), one with a side view of the infant, and one with an aerial view of the infant.

2.2.3. Procedure—At the start of the test session, infants were placed on the board and positioned within the area defined by the first semicircle. One experimenter held the infant in a stable position, supporting the infant's chest with her hands and ensuring the infant's arms and shoulders remained free to move. Once the infant was positioned, a second experimenter presented the infant with one ball at a time. Balls were of two sizes—large (21 mm diameter) and small (7 mm diameter)—, and were presented at two distances: (i) at a reachable distance (i.e., near or peripersonal space, within 5 cm from the infant), which was calculated using the average length of infants' arms ($M = 10.71$ cm, $SD = .95$ cm), and (ii) at an unreachable distance (i.e., far or extrapersonal space, 14 cm from the infant), calculated as 20% longer than the average length of the infants' arms ($M = 12. 85$ cm, $SD = 1.14$ cm). The ball was attached to a stick and presented through the window of the vertical panel in front of the infant. Infants participated in one session per day of up to 8 trials.

There were four types of trials (small and large balls presented in near and far space), each presented twice per session, in a predetermined counter-balanced order. Each trial lasted 20 seconds. If the infant interacted with the ball, the experimenter let the infant manipulate the ball for few seconds, after which the ball was removed. If the infant made no interaction attempt within 20 seconds, the trial was terminated and the ball removed. Infants were tested twice per week, for 4 weeks, between days 7 and 30.

2.2.4. Behavioral analysis—We analyzed videos frame-by-frame (33 frames per sec) using *VirtualDub* software (virtualdub.org). We scored infants' motor strategies to approach and reach the ball: (i) arm extension, if infants attempted to contact the ball by extending their arms and fingers toward the target, without stepping forward; (ii) mouth grasping, if infants leaned their torsos and heads forward, without stepping toward the target. During the movement and the approach to the target, behaviors were classified as (iii) locomotion-arm, if infants approached the target with one or more steps, followed by arm extension and ball grasping with their hands; (iv) locomotion-mouth, if infants approached the target through one or more steps, followed by grasping the ball with their mouths (see Supplementary Material, Videos S1–S4). Only the first effector used by infants to reach and grasp the ball, either the hand or the mouth, was included in the analysis. However, we assessed, for each infant, the percentage of attempts in which there was hand grasping followed by bringing the object to the mouth, or, *vice versa*, of mouth grasping followed by grasping and holding the object with the hand. This analysis included all successful grasping attempts made by infants. A grasp was considered successful when infants contacted the ball either with the mouth or the fingers flexed around the target.

We also scored infants' hand grip configurations during ball grasping and classified them as (a) hand wrap, (b) thumb-and-four-finger grip, (c) all-tips grip, (d) pad-to-pad grip, or (e) thumb-to-second-third grip (Figure 2; see also McFarlane & Graziano, 2009 for grip definitions, and Supplementary Material, Videos S4–S7). We then categorized these grip configurations depending on the parts of the hand that touched the ball. Configurations were classified as power grips (Figure 2 a–c), if the ball was held between the palm and the fingers, and with the fingers flexed around the ball, or were classified as precision grips (Figure 2 d–e), if the ball was pinched between the second or third digit and the opposing thumb (Napier, 1956). This analysis included only successful grasps.

2.2.5. Statistical Analysis—To determine whether infants' motor strategies varied across weeks and as a function of presentation distance, we applied a 4 (Motor Strategy: arm extension, mouth, locomotion-arm, locomotion-mouth) × 2 (Space: extrapersonal, peripersonal) × 3 (Age: week 2, week 3, week 4) two-way repeated measures analysis of variance (ANOVA) on the mean frequency of successful grips.

To investigate whether infants' reaction times from the presentation of the target to the onset of reaching movements varied across weeks as a function of the effector used to grasp the ball and the presentation distance, we applied a 2 (Effector: hand, mouth) × 2 (Space: extrapersonal, peripersonal) × 3 (Age: week 2, week 3, week 4) two-way repeated measures ANOVA on the mean latency of successful grips.

To investigate whether infants' grip configurations changed across weeks and according to ball size, we carried out a 2 (Grip Type: power, precision) × 2 (Ball Size: small, large) × 3 (Age: week 2, week 3, week 4) two-way repeated measures ANOVA on the mean frequency of successful grips.

To adjust for multiple comparisons, we performed post-hoc comparisons with Bonferroni corrections. Since the data were non-normally distributed, they were square root transformed prior to analysis.

3. Results

3.1. Motor Strategy

Overall, the present results revealed that infant monkeys perceived objects at varying distances in space, and successfully reached and grasped objects by using either their hands or mouths as effectors. Moreover, it is interesting to note that infants often performed hand-mouth coordinated actions to explore the objects. In fact, we observed several occurrences in which infants reached for objects using their hands first, followed by bringing the object to their mouth, or they approached the object with their mouth first, followed by their hand grasping and holding the object. In peripersonal space, infants' mean percentage of hand-mouth actions was 21.4 ($SD = 5.9$) in the second week of life, 29.7 ($SD = 8.7$) in the third week, and 16.6 ($SD = 7.0$) in the fourth week, whereas in the extrapersonal space, it was 8.0 ($SD = 3.2$) in the second week, 15.4 ($SD = 3.1$) in the third week, and 12.5 ($SD = 4.1$) in the fourth week.

Over the course of development, infants' use of behavioral strategies to obtain objects changed, suggesting that critical improvements in sensorimotor integration were occurring. Analysis of motor strategies revealed main effects for strategy, $F(3, 15) = 17.85$, $p < .001$, $\eta^2_p = .543$, space, $F(1,15) = 15.76$, $p = .001$, $\eta^2_p = .512$, and week, $F(2, 15) = 4.76$, $p = .016$, $\eta^2_p = .241$, showing that infants performed more successful grips in the peripersonal space ($M = .657$, $SD = .031$) than in extrapersonal space ($M = .559$, $SD = .041$, $p = .001$), and that the frequency of grips increased significantly from week 2 ($M = .434$, $SD = .073$) to week 3 ($M = .700$, $SD = .060$, $p = .001$), and from week 3 to week 4 ($M = .691$, $SD = .066$, $p = .049$).

We found an interaction between strategy and space, $F(3, 15) = 27.07$, $p < .001$, $\eta^2_p = .643$, which indicates that infants reached and grasped the ball by simply extending their own hand or mouth more in the peripersonal space (hand: $M = 1.10$, $SD = .091$; mouth: $M = .499$, $SD = .077$) than in the extrapersonal space (hand: $M = .286$, $SD = .062$, $p < .001$; mouth: $M = .042$, $SD = .028$, $p < .001$), whereas locomotion followed by hand or mouth grasp was more frequent in the extrapersonal space (locomotion-arm: $M = .788$, $SD = .116$; locomotion-mouth: $M = 1.121$, $SD = .147$) than in the peripersonal space (locomotion-arm: $M = .142$, $SD = .068$, $p = .001$; locomotion-mouth: $M = .884$, $SD = .099$, $p = .026$).

Moreover, there was an interaction between strategy and week, $F(6, 15) = 3.20$, $p = .007$, $\eta^2_p = .176$, in which the use of the arm increased from week 2 ($M = .232$, $SD = .069$) to week 3 ($M = .724$, $SD = .142$, $p = .014$), and from week 2 to week 4 ($M = 1.127$, $SD = .175$, $p = .001$), but there was no difference between week 3 ($M = .724$, $SD = .142$) and week 4 ($p = .127$). Similarly, the use of the hand in association with locomotion increased from week 2 ($M = .289$, $SD = .094$) to week 3 ($M = .609$, $SD = .117$, $p = .047$).

Finally, we found a three-way interaction among strategy, space, and week, $F(6, 15) = 2.65$, $p = .020$, $\eta^2_p = .150$ (Figure 3). Post-hoc comparisons revealed that in peripersonal space there was a progressive increase of the use of the arm from week 2 ($M = .463$, $SD = .138$) to week 3 ($M = 1.215$, $SD = .175$, $p = .009$), and from week 2 to week 4 ($M = 1.631$, $SD = .227$, $p = .001$), with a parallel decrease of the use of locomotion in association with the mouth from week 3 ($M = 1.140$, $SD = .115$) to week 4 ($M = .655$, $SD = .184$, $p = .049$). Similarly, in extrapersonal space, infants exhibited an increase in successful grips performed with the hand, although still in combination with locomotion, from week 2 ($M = .427$, $SD = .146$) to week 3 ($M = 1.030$, $SD = .205$, $p = .029$), and from week 2 to week 4 ($M = .908$, $SD = .168$, $p = .034$), but there was no difference between week 3 ($M = 1.030$, $SD = .205$) and week 4 ($M = .908$, $SD = .168$, $p = .586$). Across all the three weeks, infants used their arm more in peripersonal space (week 2: $M = .463$, $SD = .138$; week 3: $M = 1.215$, $SD = .175$; week 4: $M = 1.631$, $SD = .227$) than in extrapersonal space (week 2: $M = .00$, $SD = .00$, $p = .004$; week 3: $M = .233$, $SD = .160$, $p < .001$; week 4: $M = .623$, $SD = .168$, $p < .001$). Similarly, across all weeks, infants' mouths were used more in peripersonal space (week 2: $M = .598$, $SD = 162$; week 3: $M = .500$, $SD = .129$; week 4: $M = .401$, $SD = .136$) than in extrapersonal space (week 2: $M = .00$, $SD = .00$, $p = .002$; week 3: $M = .063$, $SD = .063$, $p = .004$; week 4: $M = .063$, $SD = .063$, $p = .021$). In contrast, infants' frequency of locomotion-arm, both in the third and fourth week of life, was higher in far space (week 3: $M = 1.030$, $SD = .205$; week 4: $M = .908$, $SD = .168$) compared to near space (week 3: $M = .188$, $SD = .101$, $p = .002$; week 4: $M = .088$, $SD = .088$, $p = .002$). Finally, in the fourth week of life, infants' frequency of locomotion followed by mouth contact was higher in far space ($M = 1.157$, $SD = .229$) compared to near space ($M = .655$, $SD = 184$, $p = .004$).

There were no other statistically significant effects, $ps > .05$.

3.2 Reaction Times from Stimulus Presentation to the Onset of Reaching Movement

Analysis of reaction times revealed main effects for space, $F(1, 15) = 8.06$, $p = .012$, $\eta^2_p = .35$, and week, $F(2, 15) = 5.93$, $p = .007$, $\eta^2_p = .283$, showing that infants were faster in the peripersonal space ($M = 7.44$, $SD = .076$) than in extrapersonal space ($M = 9.76$, $SD = 1.01$, $p = .012$), and that the reaction times to grasp the ball decreased significantly from week 2 ($M = 11.86$, $SD = 1.21$) to week 4 ($M = 6.45$, $SD = 1.19$, $p = .008$), while the difference between week 2 and week 3 only approached significance ($M = .7.49$, $SD = 1.51$, $p = .068$).

We found an interaction between effector and week, $F(2,15) = 3.83$, $p = .33$, $\eta^2_p = .203$, which indicates that the reaction time to grasp the ball with the hand decreased significantly from week 2 ($M = 15.04$, $SD = 1.53$) to week 3 ($M = 8.15$, $SD = 1.99$, $p = .036$) and from week 2 to week 4 ($M = 3.91$, $SD = 1.45$, $p < .001$), whereas there were no differences in mouth reaction times across weeks (week 2 $M = 8.69$, $SD = 1.68$; week 3 $M = 6.82$, $SD = 1.69$; week 4 $M = 8.99$, $SD = 1.85$, $ps > .05$). Moreover, infants were faster when grasping the ball with their hand than with their mouth in week 2 (hand $M = 15.04$, $SD = 1.53$; mouth $M = 8.69$, $SD = 1.68$, $p = .013$) and week 4 (hand $M = 3.91$, $SD = 1.45$; mouth $M = 8.99$, $SD = 1.85$, $p = .038$), whereas no difference between the two effectors was found in the third week (hand $M = 8.15$, $SD = 1.99$; mouth $M = 6.82$, $SD = 1.69$, $p > .05$).

3.3. Hand Grip Repertoire

Infant macaques showed five different hand configurations during ball grasping. As we mentioned (see paragraph 2.2.4.), these hand configurations were classified as (a) hand wrap, (b) thumb-and-four-finger grip, (c) all-tips grip, (d) pad-to-pad grip, or (e) thumb-to-second-third grip (Figure 2). However, we observed that in the second week of life infants relied on a small grip repertoire exhibiting only three configurations (i.e. hand wrap, thumb-to-four-finger, thumb-to-second-third). More specifically, starting from day 7, 11 infants out of 16 infants grasped the target using a whole hand configuration, whereas, starting from day 11, only 3 out of 16 infants used either thumb-to-four finger grip or thumb-to-second-third grip. In the third week, a greater number of infants continued to use these grip configurations: all infants grasped the object by using a hand wrap configuration, 14 infants showed the thumb-to-second-third grip, and 8 infants performed the thumb-to-four finger grip. Concurrently, 4 infants enlarged their grip repertoires, starting to show other configurations such as all-tips grip and pad-to-pad grip. Finally, in the fourth week, the full range of grip types was evident, and all infants performed hand wrap and thumb-to-second-third grips, whereas configurations, such as thumb-to-four finger, all-tips, and pad-to-pad were used by 10, 7, and 7 infants, respectively.

3.4. Hand Grip Configurations According to the Size of the Object

3.4.1. Grips in Peripersonal Space—Analysis of infants' grip configurations when the ball was in near space revealed main effects for grip type, $F(1, 15) = 12.18$, $p = .003$, $\eta^2_p = .448$, ball size, $F(1,15) = 10.41$, $p = .006$, $\eta^2_p = .410$, and week, $F(2, 15) = 13.12$, $p = .000$, $\eta^2_p = .467$. Infants used more power grips ($M = .692$, $SD = .078$) than precision grips ($M = .300$, $SD = .057$), reached and grasped the ball more when it was large ($M = .595$, $SD = .042$) than when it was small ($M = .397$, $SD = .057$), and increased the number of successful grips from week 2 ($M = .207$, $SD = .069$) to week 3 ($M = .572$, $SD = .055$, $p = .004$), and from week 2 to week 4 ($M = .710$, $SD = .085$, $p = .001$).

We found an interaction between grip type and ball size, $F(1, 15) = 10.61$, $p = .005$, $\eta^2_p = .414$, which indicates that infants used the power configuration more for the large ball ($M = .911$, $SD = .088$) than for the small ball ($M = .473$, $SD = .098$, $p = .001$), whereas precision grip was used equally for the large ($M = .279$, $SD = .064$) and the small balls ($M = .321$, $SD = .080$, $p = .645$) (Figure 4a). Moreover, the power configuration ($M = .911$, $SD = .088$) was used more than precision grip for grasping the large ball ($M = .279$, $SD = .064$, $p < .001$), whereas the two configurations were equally used for grasping the small ball (power: $M = .473$, $SD = .098$; precision: $M = .321$, $SD = .080$, $p = .290$).

There were no interactions between grip type and week, $F(2, 15) = 3.11$, $p = .059$, ball size and week, $F(2, 15) = 1.45$, $p = .256$, or among grip type, ball size, and week, $F(2, 15) = 0.90$, $p = .414$.

3.4.2. Grips in Extrapersonal Space—Analysis of infants' grip configurations when the ball was in far space revealed main effects for ball size, $F(1,15) = 14.75$, $p = .002$, $\eta^2_p = .496$, and week, $F(2, 15) = 19.24$, $p < .001$, $\eta^2_p = .562$, indicating that infants reached and grasped the ball more when it was large ($M = .516$, $SD = .040$) than when it was small (M

= .310, SD = .061, p = .002) and increased the number of successful grips from week 2 (M = .100, SD = .034) to week 3 (M = .523, SD = .079, p < .001), and from weeks 2 to 4 (M = . 625, SD = .081, p < .001). There was no main effect of grip type, $F(1, 15)$ = 4.19, p = .059.

We found an interaction between grip type and ball size, $F(1, 15)$ = 35.38, p < .001, η^2_p = . 702, in which infants used the power configuration more for the large ball (M = .825, SD = . 078) than for the small ball (M = .205, SD = .080, p < .001), and used the precision grip more for the small ball (M = .427, SD = .089) than for the large ball (M = .208, SD = .067, p = .030).

We also found an interaction between ball size and week, $F(2, 15)$ = 3.91, p = .031, η^2_p = . 207, in which the frequency of grasp attempts with the small ball increased from week 2 (M = .063, SD = .043) to week 3 (M = .458 SD = .104, p = .001), and from weeks 2 to 4 (M = . 427, SD = .098, p = .002). Similarly, grasp attempts with the large ball increased from week 2 (M = .138, SD = .063) to week 3 (M = .588 SD = .081, p < .001), and from weeks 2 to 4 (M = .824, SD = .083, p < .001). Frequencies of grasp attempts with both the small and the large ball did not differ between weeks 3 and 4 (ps > .05).

Furthermore, we found a three-way interaction between grip type, ball size, and week, $F(2, 15)$ = 4.97, p = .016, η^2_p = .242. Post-hoc comparisons showed that infants started using the power grip more often for the large ball (M = .925, SD = .149) than for the small ball (M = . 276, SD = .126, p = .001) in the third week of life. Similarly, starting from the third week, they used the precision grip more for the small ball (M = .640, SD = .151) than for the large ball (M = .250, SD = 112, p = .025). Moreover, the use of power grip for grasping the large ball increased progressively from week 2 (M = .276, SD = .126) to week 3 (M = .925, SD = . 149, p = .003) and from week 3 to week 4 (M = 1.273, SD = .146, p < .001). Likewise, there was an increase in the use of precision grip for the small ball from week 2 (M = .063, SD = . 063) to week 3 (M = .640, SD = .151, p = .002) and from week 3 to week 4 (M = .578, SD = .154, p = .003) (Figure 4b).

There were no other statically significant differences, ps > .05.

4. Discussion

To successfully reach for an object, infants need information about: the object's position and orientation in space, and its properties (e.g., size); the position and movements of their arms and hands relative to their bodies (i.e., proprioception); and the position of their arms and hands relative to the object. The results of the present study reveal that infant monkeys perceive objects at varying distances in space and use this information to plan their motor strategies and adjust their hand configurations. Over the course of the first weeks of life there are changes in infants' use of behavioral strategies to obtain objects, which may reflect critical improvements in their motor development and sensorimotor integration. This developmental trajectory seems to occur in parallel with body schema modifications and, consequently, with space perception.

Thus, data reported in the current study support the idea that infants' reaching-grasping behaviours are voluntary and goal-directed, in contrast with the traditional description of

newborn infants' behaviors as reflexes. By definition, reflexes are involuntary, automatic and fixed responses, and therefore stereotyped, not altered by learning, and not adjusted to meet a goal. Our preliminary behavioural observations (see paragraph 2.1.2) are in agreement with previous experiments in infant rhesus monkeys (Castell & Sackett, 1972; Milbrath 1968; Mowbray & Cadell, 1962), demonstrating that a stage of involuntary grasp response is present on the first 10 days of life, and that after this time grasping becomes largely voluntary. Moreover, these studies reported that infants' abilities to respond to visual stimuli, and to visually follow objects, rapidly develop in the first postpartum days (days 4–7; Harlow et al., 1956). In addition, we showed evidences that the reaching-grasping behaviours recorded in this study are voluntary, goal-directed, and flexible. Indeed, we report that with age infant demonstrate an improved capacity to successfully grasp objects and a decrease in errors (see Supplementary Results), suggesting that learning is occurring. This result is incompatible with the interpretation that these behaviors are reflexes. Furthermore, infants often made postural adjustments before starting a reaching movement, and before initiating an arm movement, they looked at the target toward which the action was directed (see Supplementary Material, Videos S1–S7).

4.1. Perception of Object Distance and Infants' Motor Strategies

Whether an object is reachable or not is determined by both the object's characteristics and by the actor's capacity to act (i.e., motor ability) in the environment (Rochat & Goubet, 1995; Rochat, Goubet, & Senders, 1999; Turvey, 1992). In the present study, infants made more reach-grasp attempts when objects were presented in peripersonal space, compared to extrapersonal space, suggesting that, from early in development, monkey infants may have perceived whether objects were reachable, and discriminated objects in extrapersonal and peripersonal space. This interpretation is in agreement with studies in human infants, which suggested that, from the moment infants begin to reach, around 4–5 months, they also detect the affordable distance at which an object is reachable (Cruikshank, 1941; Field, 1976; Rochat & Goubet, 1995; Rochat et al., 1999).

Anecdotally, we observed that in the first week of life, infants made some attempts to grasp objects while clinging to the surrogate. This observation extends those previously reported (Hinde et al., 1964; Nelson et al., 2011), but also shows that macaque infants' capacity to grasp objects is precocious and develops earlier than previously thought. In particular, early attempts to grasp are displayed by infants already in the first week of life and appear to become more frequent starting from the second week. These findings indicate that significant modifications in motor development and visuo-motor coordination are occurring between the first and the second week of life. These changes might be critical for the development of body perception in relation to the capacity of the individual to act on objects and to navigate through space.

Although the timing of development in the use of the hand and the mouth is different between human and monkey infants (Antinucci, 1990; Spinozzi & Natale, 1986; Vauclair, 1984, Bard & Vauclair, 1984), we observed interesting similarities in their pattern of emergence. Infant monkeys approached and grasped objects with their mouths earlier in development than they grasped with their hands. This mouth grasping was common in the

second week of life, during which time they explored objects with their mouths, both in peripersonal and extrapersonal space. Clearly, the mouth predominated as the main effector to reach and grasp the target. From the third week of life, hand grasping became more prominent and skilled, even if the pattern of object exploration with the mouth continued to be used concurrently with hand prehension. Moreover, with age, in peripersonal space, as hand prehension became more frequent and precise, mouth grasping decreased. It is interesting to note that previous pioneering anecdotal observations by Hinde and colleagues (1964) reported that infant macaques started to make grasp attempts in the first week of life and that the mouth is often used to contact objects during the second week of life. Although this study is mainly observational, and lacks quantitative analysis, it is, however, consistent with our findings.

Similarly, in humans, the mouth is used as the first haptic exploration tool, and with age this function is lost (McCall, 1974; Ruff, 1984; Rochat & Goubet, 1995; Rochat et al., 1999). During the first six months of life, human infants progress from oral (proximal) preference to arm movements (distal) to reach objects. By the end of the first year, instances of oral exploration decrease, as fine object manipulation and visuomotor coordination increase (McCall, 1974; Ruff, 1984; Rochat & Goubet, 1995; Rochat et al., 1999).

The present findings thus indicate that in monkeys, similarly to humans, there is a tight link between hand and mouth actions, which are often coordinated in order to explore objects. In fact, we observed that infants often reached for objects using two types of coordinated actions. In the first type, infants used their hands first, followed by bringing the object to the mouth; in the second type, infants approached the object with the mouth first, followed by the hand grasping and holding the object. Interestingly, these motor patterns involving the coordination between the hand and the mouth occurred prior to the development of independent locomotion, probably reflecting motor synergies present even before birth, as demonstrated by ultrasonographic research in human fetuses (Butterworth & Hopkins, 1988; De Vries, Visser, & Prechtl, 1984; Lew & Butterworth, 1997; Reissland, Francis, Aydin, Mason, & Schaal, 2013).

From a neurophysiological perspective, parietal-premotor cortical circuits support hand-mouth coordination (Graziano, Taylor, & Moore, 2002; Rizzolatti et al., 1988). In particular, in both the ventral premotor cortex and the posterior parietal lobule there are neurons that code actions performed with either the hand, or the mouth, or both, thus suggesting that often such coding is not limited to a movement performed with a specific effector. Interestingly, the motor representations of hand and mouth, both in the ventral premotor cortex and the posterior parietal lobule, are adjacent and partially overlapping (Buccino et al. 2001; Ferrari, Gallese, Rizzolatti, & Fogassi 2003; Rozzi et al., 2008), thus further supporting the hypothesis that the coordination of hand and mouth actions relies on neurophysiological mechanisms that, at the cortical level, are functionally and anatomically connected.

In addition to these studies, others indicate that, within these cortical sectors, visuomotor neurons are also present and they activate both when a stimulus is applied to the body surface (around the face or the arm) and when a visual stimulus is approaching or moving

away from that body part (Fogassi et al., 1996; Gentilucci et al., 1988; Graziano, 2006; Maranesi et al., 2012; Rozzi et al., 2008). The co-occurrence of these bimodal neurons with motor neurons within the same cortical sector, and the anatomical connection and proximity of the cortical areas containing such neurons, supports the idea of a tight link between space coding and goal-directed movements.

Another factor to consider is the challenge posed by postural adjustments and improved locomotion coordination during development. As already noted by Piaget (1954) and other psychologists (Bremner, Holmes, & Spence, 2008), infants' capacity to autonomously move in three-dimensional space expands not only their motor possibilities but also their capacity to plan movements in time and space. These landmark developmental changes are accompanied by the maturation of the skeleton-muscle structure and body biomechanics. For example, changes in the body (e.g., skeleton growth) alter the perception of external space (Maravita, Spence, & Driver, 2003), therefore requiring a parallel update of the body schema (Bremner, Mareschal, Lloyd-Fox, & Spence, 2008; Bremmer et al., 2008; Spence, Pavani, & Driver, 1998; Pavani, Spence, & Driver, 2000; Shore, Spry, & Spence, 2002). Thus, infant monkeys' improved reach-grasp performance (i.e., increase with age in number of reach-grasp attempts with the hand), starting from the second week of life, should be considered in terms of their capacity to overcome the constraints posed by their posture and increased sensorimotor coordination of their bodies, and especially their arms. Our results in fact showed that, between the second and fourth week, there was a change in infants' strategies to reach objects in peripersonal space, with increases in the use of the arm and decreases in movements of the body and mouth toward the target. Parallel to this, there was a change in infants' motor strategy in extrapersonal space, with increases in arm actions associated with locomotion.

These data seem to suggest that infants encode spatial locations in relation to their opportunities to generate active movements towards objects located at varying distances. It is possible that the sensorimotor experience of reaching and grasping objects, displayed in the second week of life, support infants' construction of their body representation, centered mainly on the mouth, but also more generally to the whole body. At this age, infants reach objects primarily through body movement and extension toward objects, which are then grasped by the mouth. Subsequently in development, by the third and fourth weeks of life, infants' increased use of their arms and hands to reach objects may modify their space representation in relation to the enlarged possibilities of the motor system.

This *sequela* of events in the use of different effectors likely facilitates the process of discriminating near and far space in relation to the different body effectors. During the first weeks of life, the improved body motor maturation of the skeleton and of general postural adjustments, allowed infant macaques in the present study to improve their arm motor skills, thus expanding their motor possibilities to reach objects outside the near space by better coordinating their use of their arms with their body (Rochat et al., 1999).

Our data clearly demonstrate that, from the third week of life, but likely not earlier, infants are accurately discriminating distances and choosing appropriate motor strategies for varying distances, reaching with only their arm or moving their entire body, thus suggesting

that only at a later stages of early development infants appear to code space in coordinates that can also include their arms. With age, the gradual increase in the use of the arm to actively reach for objects seems to be crucial for inducing changes in the body schema and for remapping near-space representations based on an arm-centered coordinate system.

Neurophysiological work in monkeys reveals specific brain areas in the parietal and premotor cortices that code for peripersonal space and containing neurons showing both motor and visuotactile properties (Fogassi et al., 1996; Graziano & Cooke, 2006; Graziano, Gross, Taylor, & Moore, 2004). Such representations are adjacent to the cortical motor representation of the hand and the arm, thus suggesting a neuro-anatomical connection and a possible functional link in the way space representations for the mouth and arm are constructed during development. Thus, it is likely that arm, body, and face cortical motor maps are integrated, even though their representations might still have independent (although partially overlapping) anatomical distributions and different functional roles in sensorimotor integration (Rizzolatti & Luppino, 2001). Our data seems to suggest such independence in the timing of their developmental emergence, with body and face representations developing first, followed by arm representations.

4.2. Grip Types for Targets of Varying Size and Distance

To grasp objects, infants need to shape their hands to match the three-dimensional structure of the object. This behavior requires a transformation from the visual representation of the object's geometrical properties to the motor commands acting on the muscles of the hand. Our results revealed that, over the course of the first weeks of life, infants performed adjustments in their reaching and hand grasping configurations, depending on the objects' size and distance. As early as the second week of life, infants showed the ability to used power and precision grips, even though their capacity to display these hand motor patterns did not reach the level of a fully matured adult configuration.

Previous studies in infant monkeys failed to describe fine and skilled hand and digit movements in the first month of life. The absence of such descriptions might be related to the hypotheses concerning the maturation and function of the pyramidal tract and its direct connections to the lateral motor-nuclei of the spinal cord (Evarts, 1981; Porter & Lemon, 1993). Both in humans and monkeys, the result of anatomical and electrophysiological studies support the idea that cortico-motoneuronal (CM) connections, which arise from the primary motor area, are important in the development of dexterity and in the central control of relatively independent finger movements (RIFM) (Kuypers, 1981; Dum & Strick 1991; Porter & Lemon, 1993). Kuypers (1962) suggested that the inability of infant monkeys to perform RIFM at birth was in part attributable to the immaturity of the CM projections. Lawrence and Hopkins (1976) reported that infant macaques started reaching at 3–4 weeks, but the earliest signs of RIFM occurred at 2–3 months, with a mature pattern at 7–8 months. Clearly, the study by Lawrence and Hopkins, although conducted on a small number of infants, contrasts the early hypothesis that a fully matured corticospinal tract is needed to display RIFM. Moreover, when in the adult monkey the monosynaptic connections are experimentally interrupted, dexterous movements can still be present as well as corticomotoneuronal excitation mediated through disynaptic pathways (Sasaki et al., 2004).

Galea and Darian-Smith (1995) reported that performance on a reach-and-grasp test by a group of young macaques approached adult levels by 6 months and correlated with the emergence of an adult-like distribution of cortical motor areas contributing to the corticospinal tract. Armand and colleagues (1997) showed that the CM projection was weak at birth and, although it developed rapidly in the first few postnatal months, it was not fully mature until the second year of life. This study demonstrates that the process of maturation of CM pathway is complex and follows a slow developmental trajectory. Furthermore, transcranial magnetic stimulation (TMS) studies exploring the maturation of the corticospinal system in the infant macaque (Eyre, Miller, & Ramesh, 1991; Flament, Hall, & Lemon, 1992; Müller, Hömberg, & Lenard, 1991: Müller, Ebner, & Hömberg, 1994; Olivier, Edgley, Armand, & Lemon, 1997) reported that the earliest component of electromyogram (EMG) responses to TMS, which in the adult is mediated by the CM system (Edgley, Eyre, Lemon, & Miller, 1990; Baker, Olivier, & Lemon, 1994), could not be obtained before 2–3 months of age. According to some authors, this finding supports the idea that functional CM connections must be established for the capacity to perform fine finger movements. Together these findings do not provide a univocal picture of how the maturation of the corticospinal tract in the first months of development supports the emergence of more complex skilled hand movements. Although it seems that there is a relation between these two aspects, the course of the changes occurring at behavioral, neuroanatomical, and physiological levels, especially in the first months of life, remain poorly understood.

Thus, in the absence of corticospical connections, it might be expected that there would be no hand and digit movements of interest prior to the emergence of a fully mature precision grip. Conversely, the present study provides a novel description of the development of different grasping configurations in early infancy, suggesting a gradual development of the motor system's structure and function. It should be noted that the early behaviors described in the current study are certainly not the equivalent of the well-developed reaching-grasping behaviors seen later in infancy or in mature individuals. As described in the Behavioral Analysis paragraph (2.2.4), we classified hand configurations as power and precision according to Napier's definition (1960), which differs from the definition used by Lawrence and Hopkins (1976) for RIFM. In fact, the precision grip described by Napier (1960) is not considered a complex movement dependent upon fibres passing in the pyramidal tracts (Hepp-Reymond & Wiesendanger, 1972).

Nevertheless, it is possible that the occurrence of the developmental changes in the grasping patterns displayed by infants in this study may be mediated by the developing pyramidal tract and the maturation of functional CM connections, which although they are weak in the first month of life, are nevertheless present with a small proportion depending on the selected area of the lamina IX (Armand et al., 1997). Interestingly, more recent electrophysiological and anatomical studies in humans suggest that direct connections of the pyramidal tract to motor neurons are established before birth (Eyre, Miller, Clowry, Conway, & Watts, 2000). Our observations of the early development of different grasping patterns might suggest that also in monkeys the refinement of CM connections occurred prenatally, which would also explain the precocious motor development displayed by newborn macaques compared to other animals (Martin, 2005), and might account for why infant macaques begin reaching in their first weeks of life (Hinde et al., 1964; Lawrence &

Hopkins, 1976). However, several other lines of evidence suggest that the development of segmental corticospinal terminations in monkeys follow a different pattern (Kuypers, 1962; Armand et al., 1997). Between birth and about 8 months, as the corticospinal tract increased in its overall size (Heffner & Masterton 1983; Nudo, Sutherland, & Masterton, 1995), along with the emergence of corticospinal terminations in the ventral horn, where the lateral motor-nuclei are located (Kuypers, 1962; Armand et al., 1997), monkeys begin to move their fingers more independently and develop precision grip (Lawrence & Hopkins 1976; Flament et al., 1992; Galea & Darian-Smith, 1995).

However, the maturation of the CM system is only one factor in the development of hand motor skill. Although the establishment of functional CM connections may be an important milestone in the development of motor skills, this aspect should be considered as one of many markers of the developmental process and may not parallel other measures of functional maturity of the motor system. It is possible that, at this early developmental stage, other elements of the infant's motor system are maturing and that the emergence of infant's correct hand shaping (to match three-dimensional objects) also involves parieto-frontal circuits and connections between the anterior intraparietal (AIP) area and ventral premotor cortex (Murata, Fadiga, Fogassi, Gallese, Raos, & Rizzolatti, 1997; Rizzolatti et al., 1988). Parieto-frontal circuits provide an anatomical basis for the transformation of sensory information into actions (Matelli & Luppino, 2001; Rizzolatti et al., 1998). Both the ventral premotor cortex and AIP contain neurons that code for selective hand manipulations, grasping movements, and various visual characteristics of three-dimensional objects (Rizzolatti et al., 1988; Murata et al., 1997). Jeannerod and colleagues (1995) suggested that this circuit may transform the three-dimensional characteristics of objects from sensory information into the appropriate hand movements for grasping. Interestingly, although these areas have a weak direct influence on the spinal motor neurons, with the majority of their corticospinal neurons terminating in the intermediate zone (Dum & Strick, 1996; 2002), they nevertheless can influence motor output at the level of both the primary motor area and the spinal cord (Dum & Strick, 1991). Indeed, several reports demonstrate that the ventral premotor area can influence hand motor function through both corticospinal projections and corticocortical projections to the primary motor cortex. Stimulation of the macaque ventral premotor cortex, which by itself evoked little or no detectable corticospinal output (Maranesi et al. 2012), can produce a robust modulation of motor outputs from the primary motor cortex (Shimazu Maier, Cerri, Kirkwood, & Lemon, 2004) in a muscle- and grasp-specific manner (Prabhu et al., 2009).

Together, these findings suggest that parieto-premotor circuits and the corticospinal system might work in parallel in the control of motor functions. However, these two systems might follow two different developmental patterns, with the former emerging earlier than the latter. Probably, the early motor behaviors exhibited by our infant monkeys and the sensory consequences of their actions are crucial in shaping the developing patterns of connection between motor cortex neurons and spinal motor circuits and the functional organization of the motor system. This mechanism would help to refine and stabilize mature connections and therefore to expand infant's behavioural repertoire and motor planning capabilities. Accordingly, the longer corticospinal development could reflect the need to adapt to

changing motor control demands as the infants grow throughout life (Martin, 2005), thus supporting more independent finger movements and fine hand skills.

Moreover, it is interesting to note that two different developmental patterns of grasping emerged when targets were located in near and far space. When tested in peripersonal space, infants used the power grip more often when the ball was large, but they did not preferentially use a specific configuration when the ball was small. In fact, when a small ball was presented in the peripersonal space, infants kept using a whole hand configuration to grasp the object. One interpretation is that, in near space, the whole hand configuration can be used to successfully take possession of the object and postural stability may facilitate this motor pattern, which, in terms of sensorimotor efforts, is more efficient and less demanding. In fact, the advantage of opening the hand more fully is that it requires less endpoint accuracy relative to precision grips (von Hofsten & Rönnqvist, 1988). This behavior could be adaptive, since a fully opened hand will optimize the possibility of capturing the object efficiently (Wing, Turton, & Fraser, 1986). Thus, preparatory adjustments to object size are less crucial than are preparatory adjustments to object distance.

Conversely, our data showed that infants' correct configuration of their hands and performance of precision grips when the ball was small appeared only when the target was presented in extrapersonal space. This pattern emerged starting from the third week of life, during which we recorded an increased use of the arm, likely reflecting a maturation of infants' motor skills, as previously discussed. Possibly, coding the spatial relationship between more distant objects and one's body parts requires more complex processing than when objects are presented in peripersonal space (Rizzolatti & Sinigaglia, 2008). The extrapersonal task, being more demanding in terms of integration of sensory information, may have required infants to plan more effective motor strategies for reaching and grasping small objects, thus promoting the emergence of an advanced differentiation of grip configurations. In support of this idea, Bushnell and Boudreau (1993) suggest a high correspondence between unfolding perceptual abilities and the acquisition of particular motor patterns, consistent with our notion that motor limitations are of critical importance for the development and the dynamic modulation of different motor patterns (e.g., motor strategies and grip types). According to McEwan, Dihoff and Brosvic (1991), when an object is in far space and an infant has the opportunity to move toward the object, the infant will plan reaching and grasping more effectively. The dynamic interactions between objects' properties and infants' abilities to act on their environment shape and refine infants' sensori-motor systems, thus producing more effective strategies for grasping objects. Thus, through locomotion infants may acquire knowledge about the space and distance between themselves and objects, and through body movements they more accurately perceive distances and object sizes (Bertenthal, 1996).

In this regard, we hypothesize that our experimental setting and the postural support we provided to infants was more appropriate to examine the developmental aspects of infant prehension compared to previous behavioral studies on infant monkeys (e.g. Lawrence & Hopkins, 1976). Differences in the task constraints might explain why infants in the present study exhibited precocious reaching ability and the emergence of different grasping configurations.

5. General Conclusions

Our results support the view that perception and action form a closely, interconnected loop (Jeannerod, 1994), since improvements in infants' perceptual capabilities are paced by the emergence of different motor patterns and *vice versa*, motor skills are facilitated by concurrent improvement in perception (Bertenthal, Rose, & Bai, 1997; Thelen, Smith, Karmiloff-Smith, & Johnson, 1994). The behavioral results of the present study collectively suggest that in macaques' early development there are, very likely, brain mechanisms of intermodal integration of visual, proprioceptive, and motor movements similar to those described in adults (Fogassi et al., 1996; Graziano & Cooke, 2006; Graziano et al., 2004). Moreover, these findings point to the presence of an early perceptual body schema, already formed soon after birth (if not before), though only broadly defined, and subsequently modified by the acquisition and refinement of motor skills. Such modifications demonstrate the importance of early brain plasticity and of the role of early sensorimotor experience in establishing a mature capacity for coding space.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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Highlights

- We traced the development of space coding in 2 to 4 week-old infant macaques

- Infants' reaching-grasping skills improved from week 2 to week 4 of age

- Infants showed different motor strategies depending on the objects' location

- Infants adjusted their grip configurations according to the objects' size

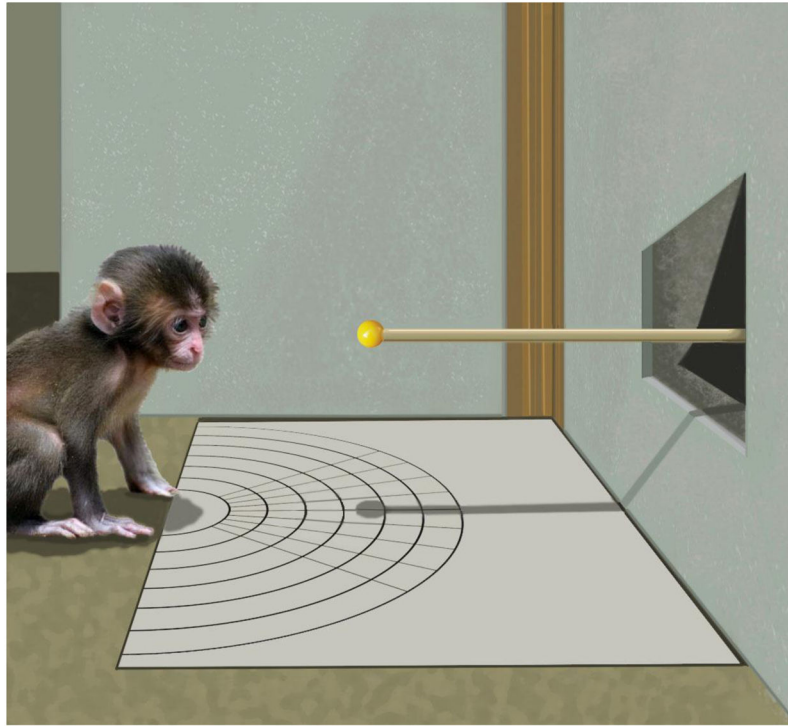- Visuo-motor transformation might start developing early in development

Figure 1.
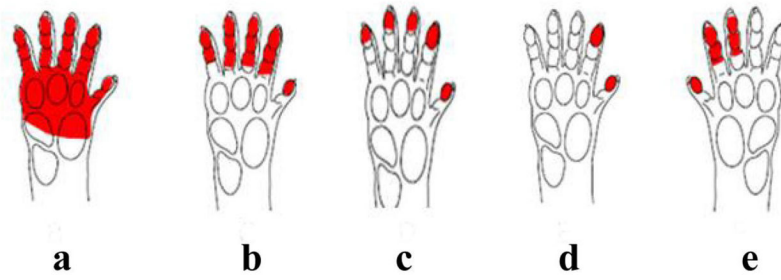Schematic illustration of the experimental setting from a side view.

Figure 2.
Hand grip configurations. (a) hand wrap, (b) thumb-and-four-finger grip, (c) all-tips grip, (d) pad-to-pad grip, (e) thumb-to-second-third grip. Configurations a, b, and c were classified as power grips; configurations d and e were classified as precision grips.
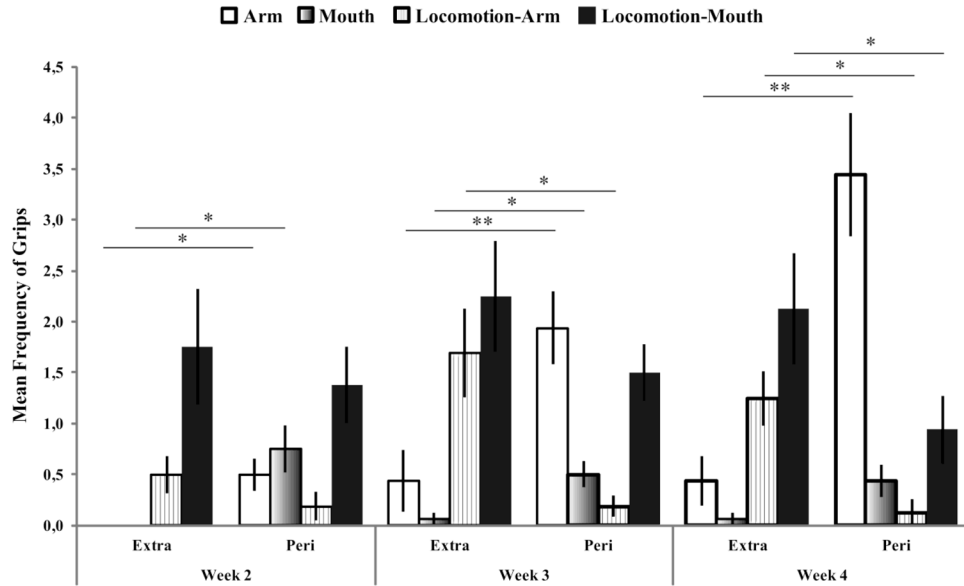
Figure 3.
Motor strategies adopted by infant macaques to successfully reach the ball in the peripersonal and extrapersonal space across age. In peripersonal space, with age, infants increased use of their arm and decreased use of locomotion-mouth. Similarly, in the extrapersonal space infants, with age, showed an increase in the frequency of successful grips performed with their hand. Across all weeks, infants used their arm more in peripersonal space than in the extrapersonal space. Similarly, infants used their mouth more in peripersonal space than in extrapersonal space. Locomotion followed by both arm and mouth grasping occurred more often in far space compared to near space. Only significant differences between extrapersonal and peripersonal space within each week are reported in the graph. Error bars show the S.E.M. $*p < .01$, $**p < .001$.
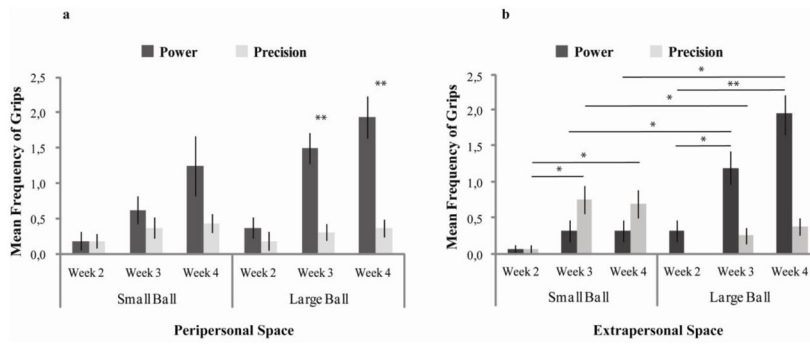
Figure 4.
Mean frequency of successful power and precision grips in (a) peripersonal and (b) extrapersonal space across weeks. In peripersonal space, infants used the power configuration more than the precision grip for grasping the large ball, whereas they equally used the two grip configurations for grasping the small ball. When balls were presented in extrapersonal space, starting from the third week, infants used the power grip more often for the large ball than for the small ball, and conversely used the precision grip more for the small ball than for the large ball. Error bars show the S.E.M. $*p < .01$, $**p < .001$.